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Review Article

Septal Region of the Rat's Brain. Ryto- and Rhemoarchitectonics

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Abstract

Objective: Analysis and generalization of literature data on the structural organization and neurotransmitters of neurons of different parts of the cerebral cortex of rats.

Methods: For this research, various literature on the relevant topic was collected and analyzed.

Results: Four groups of nuclei are located in the septal region: lateral, medial, caudal and ventral. The neurons forming them are very diverse in their neurotransmitter nature. The nucleus of the septal region forms morphofunctional connections with at least three other brain regions: the hypothalamus, the hippocampus and the amygdala.

Conclusion: The septal region is a complex complex of nuclear structures, the neurons of which are very diverse in their neuromediator nature and form numerous afferent and efferent connections with other parts of the brain. The nuclei of the septal region are involved in a wide range of neuroendocrine, behavioral and cognitive reactions and their further study in normal conditions and in experimental pathology provides a fundamental basis for integrating the results into clinical studies.

Key words: septal region; rats; brain

Introduction

The rat is a frequent object of experimental studies, including those related to the study of the structure and function of the brain. Information about the features of the structure and development of various parts of the rat brain creates a fundamental basis for various scientific projects. Some parts of the brain got its name in connection with their shape (hippocampus, amygdala), texture (striatum), localization (paraventricular nuclei) or even colour (black substance), although often at the time when they were discovered, researchers still did not know anything about their cyto- and myeloarchitectonics.

In compliance with this general trend, the medial interventricular septum of the terminal brain was named septum (Latin for "partition, wall"), in humans – septum pellucidum because of transparency [22, 23]. At the turn of the 20th century, several clusters of neuron bodies, in other words nuclei, were isolated in the septal region, and its projection connections with the hippocampus were established [15]. All the nuclei of the septal region have been the subject of very few studies and remain relatively little studied [1,18, 19, 23, 26, 27]. Even the boundaries of the septal region are still being discussed, and the ones presented in this review are based on studies by Swanson L. W. [23] with minor modifications [1, 18].

The aim of this review is to analyze and generalisation the literature data on the development, structure and functions of the septal region of the rat brain for further study in normal and experimental pathology, which will serve to create a fundamental basis for clinical research.

Anatomical organization of the septal area. There are four groups of nuclei in the septal region. The lateral group contains the lateral septal nucleus, septofimbrial and septohippocampal nuclei. The medial septal complex includes the medial central nucleus and the nucleus of the diagonal stripe. The caudal group consists of a triangular nucleus, a nucleus of the anterior commissura and a medullary stripe. Finally, the nucleus of the terminal strip forms a ventral group [20, 23]. Most of the neurons of the nuclei of the septal region form morphofunctional connections with at least three other parts of the brain: the hypothalamus, hippocampus and amygdala [18, 23].

The development of neurons of the nuclei of the septal region. The nuclei of the septal region develop from the septum formed by the rostroventromedial wall of the terminal brain. In its early stages of embryogenesis, this rudiment lies rostral to the striated and pallidal ridges and ventrally to the rostromedial cortical embryonic neuroepithelium. The nucleus of the terminal strip develops from the anterior part of the ventral angle of the horn of the lateral ventricle. The fusion of the right and left rudiments of the septal region

occurs on the 15th day of embryogenesis, then there is an intensive development of the remaining basal nuclei and anterior commissura (17th day of embryogenesis). Most neurons of the septal region are generated from the 12th to the 18th day of prenatal ontogenesis [2].

Neurons of the medial, caudal and ventral groups of nuclei develop earlier (12th-16th day of embryogenesis) than neurons of the lateral septal complex (14th–18th day of embryogenesis).

The spatio-temporal patterns of the genesis of these cell groups are also different. The medial and ventral nuclei extend in the rostral and caudal direction, while the lateral – in the lateral-medial.

The first ascending monoaminergic (serotonergic) filaments from the brainstem enter the septal region from the medial forebrain bundle on the 15th-16th day of embryogenesis. Most afferent fibers (from the hypothalamus and midbrain) develop later (from the 18th day), spreading in the lateral-medial direction [2].

The formation of connections with the hippocampus begins in embryogenesis. It is expected that the cells of the lateral group of nuclei begin to differentiate when the afferents of the hippocampus enter this nucleus. But the development of most catecholaminergic and peptidergic tracts occurs much later (on the 1st–6th day after birth). During this period, there is a decrease in the density of neuronal pericaryons in the lateral nuclei, an increase in cell size, and differentiation of organelles. Synaptic contacts between neurons of various nuclei of the septal region, as well as with the hippocampus, amygdala, hypothalamus and midbrain reach their full development by the 3rd week of postnatal development [2, 6, 7, 14, 18, 24].

Myelo- and cytoarchitectonics of the septal region nuclei. Myeloarchitectonics. Afferent and efferent fibers of the septal region form four tracts: the arch, the terminal strip, the medial bundle of the forebrain and the medullary strip.

The lateral and medial groups are connected to the hippocampus through the fimbria, the ventral group is connected to the amygdala through the terminal stripe, and the caudal group forms the medullary stripe and arch. All septal nuclei receive abundant afferent inputs from the medial forebrain bundle, and most septal neurons also form efferent fibers. The ventral group of nuclei receives afferents from the lateral region of the hypothalamus and the external parts of the pale globe, forms connections with the medial nucleus of the amygdala, ventromedial preoptic, medial preoptic and ventral premamillary nuclei of the hypothalamus. The lateral regions of the nucleus of the terminal strip form synaptic connected with the nuclear structures of the brain stem [6, 7, 18, 23, 24, 25]. Cytoarchitectonics of the lateral group of nuclei of the septal region. The lateral group is the largest cluster of neuron bodies in the septal region. The nuclei are not a homogeneous structure, the neurons in them differ in size. There are areas with different cell densities. Usually, dorsal, intermediate and ventral parts are distinguished in the nuclei of the lateral group, although these boundaries are quite controversial. The dendrites of the neurons of the nuclei of the lateral group have a developed spike apparatus, however, a special class of neurons has been found in the lateral septal nucleus, in which the spikes are located on the cell body itself. Septofimbrial neurons on average have large sizes, compared with other neurons of the nuclei of the lateral group. Axons of some neurons form collaterals, which suggests the presence of local inhibitory influences, but the types of these interneurons have not been established and described [1, 23].

Cytoarchitectonics of the medial group of nuclei of the septal region. The cytoarchitectonic boundaries between the medial septal nucleus and the nucleus of the diagonal stripe are not pronounced, both clusters of neuron bodies are connected by axons of neurons of the nucleus of the diagonal stripe.

Several types of neurons are described in the medial group of nuclei of the septal region. Some of the neurons are large, hyperchromic, while others are small fusiform [18, 20, 23].

Cytoarchitectonics of the caudal group of nuclei of the septal region. The triangular nucleus and the nucleus of the anterior commissura are formed by densely located pericaryons of neurons. The neurons of the medullary stripe are much smaller in size, their cytoplasm is only slightly stained with thionin [15, 20, 23].

Cytoarchitectonics of the ventral group of nuclei of the septal region. There are conflicting data on the histological organization of the terminal strip nucleus. It is proposed to divide the core into several sub-cores. Also, information on the exact topography of afferent and efferent connections between this nucleus and other structures (amygdala, hypothalamus, brain stem) is also ambiguous [6, 7, 23]. The classification of neurons in this area is mainly based not on morphological differences, but on the neurotransmitter nature, which will be described below.

Neurotransmitters of the septal region. The entire septal region is rich in gabaergic neurons that express glutamic acid decarboxylase [29]. However, gabaergic neurons do not form a homogeneous population, and other neurons are found among the nerve cells of the septal region.

Neurotransmitters of the lateral group of nuclei of the septal region. The chemoarchitectonics of the nuclei of the lateral group is extremely heterogeneous. The caudal intermediate part of the lateral septal nucleus is divided into four ventrodorsal oriented layers corresponding to the alternate distribution of calbindine and tyrosine hydroxylase. Using in situ hybridization, it was found that the rostral part of the lateral septal nucleus contains mainly enkephalinergic and neurotensinergic neurons, the caudal part contains somatostatinergic, and the ventral part contains neurons expressing estrogen α. The septohippocampal nucleus contains neurons expressing somatostatin and neuropeptide Y. The septofimbrial nucleus contains enkephalinergic neurons [4, 8, 11, 12].

Neurotransmitters of the medial group of nuclei of the septal region. The medial septal nucleus and diagonal stripe contain a large number of cholinergic neurons. This is a distinctive feature of this group, but chemoarchitectonics as a whole is quite complex. At least three classes of neurons that differ in the type of neurotransmitter produced are described.

1. Cholinergic neurons, which contain the enzymes cholinacetyltransferase and acetylcholinesterase, are the most numerous. In addition, cholinergic neurons contain glutamate, nitric oxide, neuropeptides. The co-expression of these molecules in cholinergic neurons or their possible interactions with acetylcholine are quite complex and not all aspects of their integration have been sufficiently studied.

2. The second group is formed by GABAergic neurons. Most of them synthesize a number of other compounds: calcium-binding proteins, and trophic factors. Some GABAergic neurons may be local interneurons.

3. Neuroendocrine neurons form the third class. They produce glutamate, acetylcholine, serotonin, dopamine and norepinephrine. Many of these neurons form afferent connections with the hippocampus [3, 4, 8, 11, 12, 13, 17].

Neurotransmitters of the caudal group of nuclei of the septal region. In the nuclei of this group, there is a wide variety of neurons of different neurotransmitter nature.

The triangular nucleus is dominated by neurons expressing calretinin, calbindin and the enzyme adenosine deaminase. Enkephalin is produced by neurons of all nuclei of the caudal group [17].

Afferent fibers from the brain stem are suitable for caudal nuclei. In particular, numerous noradrenergic synapses were found in the nucleus of the anterior commissura. In addition, this nucleus and the triangular nucleus contain cholinergic synapses containing the enzymes cholinacetyltransferase and acetylcholinesterase [4, 8, 11, 12, 13].

Neurotransmitters of the ventral group of nuclei of the septal region. Very intense expression of substance P was noted in the nucleus of the terminal strip, but, moreover, in neurons to estrogens and androgens [10].

Functions of the septal region nuclei. The nuclei of the septal region are involved in a wide range of autonomic, neuroendocrine, behavioral and cognitive reactions [21, 22].

Damage to the lateral group of nuclei leads to significant changes in emotional behavior – the so-called "septal rage". Subsequent experiments made it possible to clarify that the lateral septal nucleus is the main structure responsible for the occurrence of "septal rage" [21, 23].

Damage to the medial group of nuclei causes a number of cognitive disorders (attention and memory disorders), and also leads to desynchronization of the electrical theta activity of the hippocampus associated with memory mechanisms. GABAergic and cholinergic neurons of the medial group of nuclei of the septal region play an important role in synchronizing the bioelectric activity of hippocampal interneurons. Sometimes they are called "hippocampal pacemakers". The septal neurons themselves are under the control of the brain stem [5, 9, 16, 28].

The nuclei of the lateral, medial, caudal and ventral groups participate, including through connections with the hypothalamus, in eating and sexual behavior, the formation of dominant-subordinate relationships and parental attachment to children [21, 22, 23].

That way, the septal region is a complex complex of nuclear structures, the neurons of which are very diverse in their neurotransmitter nature and form numerous afferent and efferent connections with other parts of the brain. The nuclei of the septal region are involved in a wide range of autonomic, neuroendocrine, behavioral and cognitive reactions of the body and their further study in normal and experimental pathology provides a fundamental basis for the implementation of the results in clinical research.

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